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Review Paper

Mechanisms underlying the impacts of exotic plant invasions

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Although the impacts of exotic plant invasions on community structure and ecosystem processes are well appreciated, the pathways or mechanisms that underlie these impacts are poorly understood. Better exploration of these processes is essential to understanding why exotic plants impact only certain systems, and why only some invaders have large impacts. Here, we review over 150 studies to evaluate the mechanisms underlying the impacts of exotic plant invasions on plant and animal community structure, nutrient cycling, hydrology and fire regimes. We find that, while numerous studies have examined the impacts of invasions on plant diversity and composition, less than 5% test whether these effects arise through competition, allelopathy, alteration of ecosystem variables or other processes. Nonetheless, competition was often hypothesized, and nearly all studies competing native and alien plants against each other found strong competitive effects of exotic species. In contrast to studies of the impacts on plant community structure and higher trophic levels, research examining impacts on nitrogen cycling, hydrology and fire regimes is generally highly mechanistic, often motivated by specific invader traits. We encourage future studies that link impacts on community structure to ecosystem processes, and relate the controls over invasibility to the controls over impact.

Keywords: biological invasions; community structure; ecosystem processes; exotic plants; impact

1. INTRODUCTION

Over the past two decades, the potential for non-native species to alter ecosystem structure and function dramatically has become broadly recognized (Vitousek *et al.* 1997). Biological invasions are second only to land-use change as a cause of species endangerment in the USA (e.g. Miller 1989; Wilcove *et al.* 1998), and many individual case studies have detailed population, community and ecosystem impacts of introduced organisms (e.g. Simberloff 1995; Daehler & Strong 1993; Parker *et al.* 1999). Consequently, interest in the processes influencing the invasion of natural systems has surged. Much of this work has examined the traits that make for successful invaders (Rejmánek 1996; Rejmánek & Richardson 1996), as well as the determinants of community invasibility (Elton 1958; Levine & D'Antonio 1999; Davis *et al.* 2000). An important conclusion from this work is that, given sufficient propagule supply, few communities are likely to remain free of invasion. Thus, a logical next step is to examine the factors that regulate the impact of exotic

species once they have successfully established. Because it is the impacts of invaders and not their establishment *per se* that threaten native communities, a move towards better understanding the controls over impact may be particularly important from a conservation standpoint.

Here, we review the mechanisms underlying the impacts of exotic plant invasions in terrestrial systems. We use 'mechanisms' to mean the processes (e.g. competition, allelopathy, production of flammable biomass) that generate invader impacts (e.g. reduced diversity, increased fire frequency). Thus, our goal is not a general review of impacts, but, rather, a specific examination of the processes underlying documented effects of exotic plant invasions. Understanding these processes is essential to answering some of the most important questions in the study of biological invasions: why do only a small fraction of established exotic plants have significant impacts (Simberloff 1981; Williamson & Fitter 1996), and why do invaders have large impacts in some systems but not others? Furthermore, success in predicting which invaders are likely to exert large effects, and which communities are likely to suffer impacts is contingent upon a firm understanding of how these impacts arise. Similarly, from a restoration standpoint, we need to know which processes

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775

must be overcome if native species are to re-establish in exotic-dominated systems. Last, an understanding of the mechanisms underlying the impacts of exotic plant invasions is essential for predicting whether global climate change will exacerbate the current impacts of exotic invasions in natural systems (Dukes & Mooney 1999).

As we will show in this review, an abundance of studies have examined native community structure and ecosystem processes in areas with and without invaders. However, only a small fraction have tested the processes or pathways through which impacts develop. For example, numerous studies have documented reductions in native species diversity following invasion, yet few have documented whether these results are driven by resource competition, allelopathy or the alteration of ecosystem processes such as nitrogen cycling. This lack of attention to mechanisms may be a critical shortcoming of the invasions literature.

Here, we examine over 150 studies (see electronic Appendix A available on The Royal Society's Publications Web site) to review evidence for the mechanisms underlying the impacts of exotic plants on plant and animal community structure, nutrient cycling, productivity, hydrology and fire regimes. Papers were located through electronic searches using the keywords in each impact section and examination of the references in these citations. We use this review to explore the following questions: (i) which mechanisms of impact yield the greatest alteration of community structure or ecosystem processes; (ii) can we predict the species most likely to exert large impacts, or the systems most vulnerable to impact; and (iii) which processes underlying impacts deserve greater attention?

2. MECHANISMS OF IMPACT ON COMMUNITY STRUCTURE

(a) *Plant community structure*

Out of the 30 or more studies that examined the impact of plant invasions on the composition and diversity of native plants (see electronic Appendix A), most (more than 90%) are observational comparisons of native diversity and composition in invaded and uninvaded locations. For example, Martin (1999) found a lower richness of seedlings and saplings in areas invaded by Norway maples than in nearby uninvaded forest locations, while Pysek & Pysek (1995) found reduced species diversity in areas invaded by *Heracleum mantegazzianum* as compared with uninvaded areas in the Czech Republic. This makes understanding the mechanisms behind the impacts particularly difficult because the simple documentation of community structure in invaded and uninvaded areas reveals little about the underlying mechanisms.

Nonetheless, several studies have tested the mechanisms underlying community impacts. In one of the earliest studies of invader impacts, Vivrette & Muller (1977) showed that the crystalline iceplant, an annual invader from South Africa, dramatically altered the composition and density of coastal grassland species in California. Through a combination of resource measurements and grazer exclosures, they demonstrated that neither exploitative competition nor differential herbivory could drive this result. Measurements of the osmotic level of throughfall from the iceplant in late summer and the growth of native plant species under varying levels of sal-

inity showed that the impact was probably generated by salt accumulation beneath the plants. This was further supported by the observation that even after iceplant removal sites remained bare for several years. With these underlying mechanisms uncovered, El-Ghareeb (1991) was able to implicate similar processes in his study of the same invader in Egypt. In another mechanistic study, Dunbar & Facelli (1999) showed that *Orbea variegata*, the African carrion flower, reduced the diversity of annual plants and the performance of the dominant chenopod shrub in an Australian shrubland. Physiological measurements of the shrub in plots where *Orbea* had been experimentally removed and control plots demonstrated that *Orbea*'s impact was mediated via reduced water availability.

Although few studies rigorously tested the mechanisms underlying impacts on community structure, 20 of the studies we examined at least discussed or hypothesized mechanisms believed to underlie the impacts. Although there are limits to what can be inferred from vote-counting in reviews, 17 out of the 20 suggested that competition was the process responsible for the impact. For example, Woods (1993) suggested that competition for light was responsible for the impact of Tatarian honeysuckle on the diversity and cover of native understory herbs in a New England forest. Similar suggestions were made for the impact of forest invaders in the eastern USA (Wyckoff & Webb 1996; Martin 1999), Europe (Kwiatkowska *et al.* 1997) and tropical islands (Lavergne *et al.* 1999), and for tree invasions into fynbos shrubland in South Africa (Holmes & Cowling 1997*a*,*b*). Braithwaite *et al.* (1989) went further, and measured a reduction in light availability under the exotic shrub *Mimosa pigra*, but even they acknowledged that more work was required to identify the mechanism of impact.

Although the studies documenting impact have rarely tested the competitive mechanisms they invoke, over 20 studies have used removal, addition and neighbourhood analyses to examine the competitive interactions between native and exotic species (see electronic Appendix A). All of these documented strong competitive effects of the invasive species on the growth, reproduction and resource allocation of native residents. For example, D'Antonio & Mahall (1991) found that the succulent perennial *Carpobrotus edulis* reduced soil water availability to native shrubs in coastal chaparral and consequently reduced their growth and reproduction. Similarly, Melgoza *et al.* (1990) found that *Bromus tectorum* invasion reduced the amount of soil water available for other plants in a Nevada grassland. The resources for which the plants compete remain unclear; the studies by Melgoza *et al.* (1990), D'Antonio & Mahall (1991) and D'Antonio *et al.* (1998) described above were among the exceptions. In addition, Busch & Smith (1995) presented evidence suggesting that a combination of light and water competition underlay the effects of salt cedar, *Tamarix*, on several native riparian trees in the southwestern USA.

Although competition was by far the most commonly invoked explanation for the effects of exotic invaders on community structure, exceptions included chemical alteration of the soil through the concentration of salts (Vivrette & Muller 1977; El-Ghareeb 1991), and allelopathy (Wyckoff & Webb 1996; Gentle & Duggin 1997;

Lavergne *et al.* 1999). In addition, Holmes & Cowling (1997*a*) suggested that increased nitrogen availability caused by *Acacia* invasion may reduce the competitive performance of fynbos shrubs. Furthermore, as we describe later on (see § 3c), some of the most dramatic impacts on community structure occur through alterations in the fire regime (D'Antonio & Vitousek (1992); these are reviewed below in § 3c). Given the diversity of mechanisms hypothesized to explain the impact of invaders on community structure, before we assume that competition is the driving mechanism behind these impacts, experimental support must be provided.

(b) *Impacts on higher trophic levels*

Plant invasions can also alter community structure at higher trophic levels. We found over 30 studies that investigated the impact of plant invasions on the composition, diversity and behaviour of consumers and decomposers (see electronic Appendix A). Although most of these studies are comparative, they often reported a hypothesized mechanism that involved differences between native and exotic species in key traits. For example, Schmidt & Whelan (1999) monitored nests of robins (*Turdus migratorius*) through the breeding season in a deciduous forest in Illinois and found higher nest predation in the introduced *Rhamnus cathartica* and *Lonicera maakii* than in native shrubs and trees. This was attributed to a combination of lower nest height and the absence of sharp thorns on the exotic species. In another example, Florida flat soapberry bugs colonizing the exotic *Koelreuteria elegans* had a shorter beak length, smaller body size and produced smaller eggs with lower survivorship than individuals living on the native host, *Cardiospermum corindum* (Carrol *et al.* 1997, 1998). This could be attributed partly to the difference in the timing and quantity of seeds produced by the different plants.

Exotic plants can also modify the activity of pollinators through producing different nectar from native species. Along a European river-bank, the Himalayan *Impatiens glandulifera* produces more nectar than the native *Stachys palustris*, and receives more visitations by European bumble-bees (Chittka & Schürkens 2001). Studies such as these are typical of a literature that focuses on how different traits of native and exotic plants alter the behaviour and performance of individual animal species. Far less explored is the impact on consumer assemblages of the whole-scale alteration of plant community structure following invasions. Impacts resulting from vegetation change are beginning to be described for below-ground communities.

In hardwood forests of New Jersey, Kourtev *et al.* (1999) found higher earthworm densities under the introduced *Berberis thunbergii* and *Microstegium vimineum* than under the native *Vaccinium* spp. Although cause and effect are unclear, the soils below the exotic *Berberis* had higher nitrate concentrations and a reduced litter layer. Similar increases in earthworm density have been found under *Myrica faya* in Hawaii (Aplet 1990), which may contribute to the enhanced activity of feral pigs and the high rates of nitrogen mineralization under *Myrica* (Vitousek & Walker 1989; Aplet *et al.* 1991). Impacts such as these on soil communities most often resulted from an alteration of resource fluxes. Belnap & Phillips (2001) found lower

richness, fewer fungi and invertebrates, and higher abundances of active bacteria in sites invaded by *Bromus tectorum* in Utah, a result they attribute to *Bromus'* effects on nitrogen and carbon availability. Impacts of plant invasions on soil fauna have tremendous potential to control both resource cycling and invader dominance (Ehrenfeld *et al.* 2001), but such processes are only just beginning to be uncovered.

3. MECHANISMS OF IMPACT ON ECOSYSTEM PROCESSES

Like studies documenting the impacts of invasions on community structure, most research on ecosystem impacts is correlational. Without knowledge of what caused the differential invasion of different locations, comparisons between ecosystem processes in invaded and uninvaded areas must be treated cautiously (Scott *et al.* 2001). Nonetheless, we found that studies examining the effects of invaders on ecosystem processes tend to be far more mechanistic than their community-structure counterparts, often attributing impacts to differences in important functional traits between the invader and the resident species.

(a) *Impacts on nutrient cycling*

The effects of invasive species on nutrient cycling have been the subject of several published studies (e.g. Belnap & Phillips 2001; Ehrenfeld *et al.* 2001; Evans *et al.* 2001; Mack *et al.* 2001; Scott *et al.* 2001). The attention to nitrogen cycling, in particular, is largely the result of several dramatic examples, such as the work on *Myrica* invasion in Hawaii by Vitousek *et al.* (1987) and Vitousek & Walker (1989) and studies of *Acacia* invasions in South African Cape fynbos (Musil 1993; Stock *et al.* 1995). Over one-third of the studies that examined invader effects on nitrogen cycling were studies of nitrogen-fixing species, with a disproportionate amount of work on *Myrica* and *Acacia*. In part this is because these studies provide clear mechanisms for the impact of nitrogen-fixing plants: because of their access to atmospheric nitrogen, they tend to increase available nitrogen in the systems they invade. With this defined mechanism, the systems most likely to show impacts of nitrogen fixers might be predictable. For example, Vitousek & Walker (1989) studied invader impacts where effects should be most likely: sites lacking native nitrogen fixers and with low natural inputs of nitrogen, sparse native vegetation and young volcanic soils with high phosphorus contents that bind large amounts of organic material. Based on the ecological context and the reported mechanisms, nitrogen-rich and densely vegetated systems would not be expected to show the same impacts. Indeed, several studies failed to find consistent effects of nitrogen-fixing invaders (e.g. Haubensak 2001), or found differing effects across sites varying in parent material (Stock *et al.* 1995).

A number of studies have examined the pathways by which non-fixing species, especially grasses, alter nitrogen cycling. For example, Evans *et al.* (2001) found that *B. tectorum* reduced nitrogen-mineralization rates by having greater carbon–nitrogen and lignin–nitrogen ratios than native species, while similar litter-quality effects did not explain reduced nitrogen mineralization under invasive *Hieracium* in New Zealand grasslands (Scott *et al.* 2001).

Mack *et al.* (2001) suggest that the impacts of exotic grasses on nitrogen cycling in Hawaiian woodlands occur more through their alteration of community structure via fire than through direct invader inputs. In other grass studies, effects on nitrogen cycling were highly variable, suggesting that different mechanisms operate with different species. For example, *Hyparrhenia rufa*, a perennial tussock grass invading secondary pastures in Costa Rica, was found to lower rates of nitrogen cycling (Johnson & Wedin 1997) compared with intact uncut forest, while *Melinis minutiflora*, a perennial exotic tussock grass invading Hawaiian shrublands, was associated with higher nitrogen availability (Asner & Beatty 1996). Effects on total standing biomass and litter were similarly variable (Van Wilgen & Richardson 1985; Dascanio *et al.* 1994). The importance of testing mechanisms is further exemplified by studies of the shrub *Berberis thunbergii* and the grass *Microstegium vimineum* invading eastern USA deciduous forests (Ehrenfeld *et al.* 2001). Although both species increase nitrification and pH, the authors suggest that the shrub does so through the production of highly decomposable tissue, while the grass does so through low annual production.

Despite considerable evidence that invasions can alter nitrogen cycling, the consequences of the altered nitrogen availability for community structure are poorly demonstrated. For example, the increased availability of nitrogen following the invasion of nitrogen-fixing species might be an important pathway by which invaders alter community structure, and quite possibly favour the invasion of more exotic species (Davis *et al.* 2000). However, in most cases, the nitrogen fixers reduce local plant diversity by interfering with resident species, and seem to have no effect on the abundances of other exotic plants (Mueller-Dombois & Whiteaker 1990). As was the case with community structure impacts more generally, the mechanisms responsible for this have not been studied, but probably include shading and allelopathy. In fact, shading is more likely than altered nitrogen cycling to underlie the impact of *Myrica* and *Acacia* on surrounding plants (as in Holmes & Cowling 1997*a,b*). Only after the death of nitrogen fixers do other invaders tend to increase (e.g. Maron & Connors 1996; Adler *et al.* 1998). Thus, while it is clear that invaders can alter nitrogen cycling, it is less clear that this impact *per se* changes community structure.

(b) Impacts on hydrology

Invasive plant species alter hydrologic regimes by changing the rate or timing of evapotranspiration (ET) or runoff in a region. In our review of the hydrologic impacts of invasions, we found that such impacts were often explained by differences between invasive and native species in transpiration rates, phenology, biomass of photosynthetic tissue or rooting depth. Overall, relatively few studies (15 in our survey) have directly measured the hydrologic impacts of invasive species. Perhaps the most widely studied invader in this regard is salt cedar (*Tamarix* sp.) in southwestern North America. Zavaleta (2000) surveyed the range of studies on *Tamarix*, and suggested that invasion by this species increases ET by 300–460 mm yr^{-1}. Similarly, in annual grasslands of western North America, invasions of *Centaurea solstitialis* have increased summer water use by 105–120 mm yr^{-1}

(Gerlach 2000). In both of these examples, the authors attribute the increased ET to functional traits of the invaders, including high leaf area (*Tamarix*) and a summer active growth period (*Centaurea*).

Other invasive species decrease community water use, and in these cases the impacts are often mediated by the displacement of species that use more water. Cline *et al.* (1977) found that a *B. tectorum* community lost 70 mm yr^{-1} less soil moisture than an adjacent native-shrub-dominated community. It has been noted that stands dominated by the invader generally have shallower root systems than the native communities that they replace (Rickard & Vaughan 1988), and are photosynthetically active for a shorter portion of the year. Similarly, exotic annual grasses in California change hydrology because they competitively displace the deeper-rooting native perennials (Dyer & Rice 1999). In addition, the exotic annual grasses transpire for a short period in late winter and spring, while the native perennials transpire into the summer months. These impacts on hydrology emphasize an underappreciated pathway of impact, where effects on community structure alter ecosystem processes.

(c) Impacts on fire regimes

The mechanisms by which plant invaders alter fire regimes have been the subject of considerable study (D'Antonio 2000). Many examples of invaders increasing fire frequency occur when introduced grasses invade sites otherwise dominated by woody species, and create a more continuous fuel bed. For example, in the western USA, fire frequency has increased dramatically over the past century owing to invasion of desert shrublands by annual grasses from the Mediterranean region. This has resulted in widespread conversion of shrublands to grasslands, with effects on biodiversity (e.g. Whisenant 1990; D'Antonio & Vitousek 1992). Likewise in Hawaii, introduced grasses have increased fire frequency more than threefold in seasonally dry shrublands and woodlands, with large effects on biodiversity (Hughes *et al.* 1991; Tunison *et al.* 2001). Woody invaders may also increase fire frequency (Busch 1995; Van Wilgen & Richardson 1985), but the evidence is far weaker and more variable than for grasses.

In addition to altering fire frequency, invaders can also increase fire intensity. This tends to occur in habitats where fire has been a regular occurrence but where the invader is more productive than the native species it replaces and thereby increases fuel. Standing plant biomass and hence fuel tends to be higher as a result of the increased productivity. Greater flame lengths, higher temperatures and greater heat release have all been recorded or predicted for a variety of exotic shrubs and trees invading humid grassland, savannah or fire-prone shrubland ecosystems (Van Wilgen & Richardson 1985; Bilbao 1995; Lippincott 2000). In each case, invaders do not represent a completely new life-form, but rather increase the variety of something that already exists in the site. Thus the mechanism through which impact develops depends on whether the invader can somehow garner more resources than the resident species and turn those resources into greater above-ground standing litter production. In most cases the specific ecophysiological reasons for greater biomass production have not been identified.

Invader effects on fire regimes through alteration of fire frequency often result in complete alteration of the community, from woody-species dominance to grassland (D'Antonio & Vitousek 1992) although effects can be variable across invaded sites (D'Antonio *et al.* 2000). In contrast to the studies of impacts reviewed to this point, the literature on impacts mediated by fire strongly supports the expectation that invader impacts on ecosystem processes (e.g. disturbance regime) can strongly and possibly irreversibly affect community structure. It also supports the prediction that invaders affecting disturbance have the greatest potential to exert large impacts on ecosystems (Vitousek 1990).

4. CONCLUSIONS AND FUTURE DIRECTIONS

In our review of over 150 studies documenting the impacts of exotic plants, we found that roughly equal numbers of studies examined effects on community structure (species diversity and composition) and effects on ecosystem processes (nitrogen cycling, hydrology, etc.). Attention to the pathways by which the impacts arise, however, was much greater among the ecosystem-impact papers. The motivation for most of the ecosystem studies was an *a priori* expectation that, because of certain specified invader traits, impacts should occur via specific hypothesized pathways. For example, a number of studies examined the effects of nitrogen-fixing plants on nitrogen availability in the systems they invade, with the implicit or explicit hypothesis that any impacts would result from greater nitrogen accretion by invaders.

Studies reporting significant invader impacts are more likely to be published than those showing non-significant effects, generating a potential publication bias. However, because our focus is not on whether invaders exert impacts, but rather on the processes that underlie the impacts once they occur, we believe that this bias is relatively unimportant with respect to our review. However, it may prove important in comparisons of the magnitude of impact across mechanisms, invaders or ecosystems, and thus we qualify our discussion with this point.

Although competition was the most often implicated mechanism in the alteration of community structure and dominance, it was rarely implicated in the whole-scale transformation of a community. Rather, the most severe impacts were mediated by alteration of the fire regime (D'Antonio & Vitousek 1992). Alteration of other ecosystem processes such as nitrogen cycling failed to produce the same magnitude of impacts. In fact, one of the most interesting findings of our review is that, while invaders were often shown to alter ecosystem processes, the consequences of this for community structure were poorly tested, particularly over the long term. Another unanswered question in the ecosystem-impacts literature is the degree to which the documented impacts result simply from the addition of new functional traits brought in by the invader, or alternatively the reduction or elimination of native species (e.g. Mack *et al.* 2001).

Consistent with Vitousek (1990) and Chapin *et al.* (1994), the hypothesized mechanisms underlying impacts almost always involved functional differences between invader and resident species traits. Interestingly, such differences are more generally hypothesized to underlie the impacts of any species, native or exotic, on ecosystem processes (Chapin *et al.* 1994). Thus, like the controls over invasibility, the controls over severe impacts can be understood only by examining how invader traits compare with those of the resident community. For example, large impacts of nitrogen-fixing invaders were found in nutrient-poor ecosystems that did not previously contain nitrogen-fixing residents (Vitousek & Walker 1989; Musil 1993), yet results were more ambiguous in other systems (Haubensak 2001). We are thus pessimistic about any attempts to uncover simple rules concerning which invaders or functional groups are most likely to exert large impacts across systems, or which communities will be susceptible to impacts. This is exemplified by the highly variable effects of grasses on nitrogen cycling across systems and species (Asner & Beatty 1996; Johnson & Wedin 1997). Enhanced predictability of impacts will most probably come from matching invader traits against those of the resident community.

(a) *Future directions*
(i) *How do impacts on ecosystem processes alter community structure?*

One of the most striking findings of our review is that, while numerous studies examined how invaders altered some form of resource cycling, most often nitrogen, the consequences of this for community structure were poorly explored. In fact, effects of nitrogen fixers on plant communities, for example, was more likely to result from shading or allelopathy than alteration of nitrogen cycling. Nonetheless, the consequences of altered nitrogen cycling may be important only after invader death or removal. Thus there is a need for studies that document impacts on resource cycling but also test whether those impacts affect community structure. Factorial manipulations of the invader and the altered resource could be particularly effective in achieving this goal.

(ii) *How do communities resist impact?*

Nearly all of the studies we examined were conducted in systems where the invaders showed high potential to exert impacts. To understand more fully how impacts arise, however, we also need to explore systems that have been invaded, but suffered little impact. Understanding what allows these communities to resist the impacts of invaders is important for restoring invasion-resistant ecosystems, as well as predicting the species or systems most likely to suffer impacts. Further evidence could be provided by studies examining the differential impacts of invaders across sites (e.g. Stock *et al.* 1995; Scott *et al.* 2001). Such work is also important for understanding whether invaders exert their impacts via the same mechanisms in different systems.

(iii) *What is the relationship between the controls over invasibility and the controls over impact?*

While it is well accepted that disturbance and high resource availability increase the invasibility of communities (Davis *et al.* 2000), whether these factors also increase the intensity of impact is poorly understood. While separating the controls over invasibility from the controls over impact may have a heuristic value (Levine & D'Antonio 1999), linking these controls may prove valuable in

predicting which species will exert the greatest impacts. Studies are needed that test how invasion success is enhanced or retarded by the impacts of the invader. A number of recent studies, especially from the ecosystem perspective, have suggested that the impacts of the invasion on nitrogen cycling, fire regimes or hydrology ultimately favour its spread (D'Antonio & Vitousek 1992; Ehrenfeld *et al.* 2001). Positive feedbacks such as these may generate thresholds where impacts increase rapidly after a critical invader abundance. It may be those species whose invasive capacity and impacts are related in a positive feedback that present the greatest threats to ecological systems.

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